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Pollination Ecology of *Pedicularis muscoides* H. L. Li subsp. *himalayca* Yamazaki from Alpine Areas of Western Sichuan, China

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Abstract

The pollination ecology of small, short, and two-flowered *Pedicularis muscoides* subsp. *himalayca* was studied during its full blooming period in alpine areas of western Sichuan Province, China, part of the putative origin and diversification center of the genus. *Pedicularis muscoides* subsp. *himalayca* was nototribically pollinated exclusively by queens of four bumblebee species (*Bombus* Latr.) that foraged for nectar on flowers in an upright position. Of the four *Bombus* species, *B. friseanus* Smith occurred in the highest frequency and was the major pollinator of *P. muscoides* subsp. *himalayca*. It comprised 81% of the bumblebees collected on *P. muscoides* subsp. *himalayca*. Queen bumblebees stood on the ground while foraging on flowers, which has not previously been reported in other *Pedicularis* species. During the study period almost all the foragers were confined to the studied subspecies and very occasionally visited other associated blooming species at the study site. The low plant height; outcurved terminal flowers; short-tubed, erostrate, and copiously nectariferous flowers; corolla morphology; and highly synchronized short-blooming period of *P. muscoides* subsp. *himalayca* made this plant well adapted to pollination by queen bumblebees within a short growing season. Thus this study provides evidence for coadaptation between *Pedicularis* and bumblebee pollinators.

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Introduction

Pedicularis Linnaeus, including over 600 hemiparasite species, is the largest genus in the family Orobanchaceae (Wolfe et al., 2005) and also one of the largest genera of flowering plants in the northern hemisphere (Li, 1948). Species of *Pedicularis* grow mainly in arctic, alpine, and subalpine areas throughout the northern hemisphere, but the greatest morphological diversity and species richness in *Pedicularis* is confined to a relatively small region of East Asia (Ree, 2005), especially in the alpine areas of southwestern China and adjacent regions. The genus exhibits extremely diverse corolla morphology that is likely unequalled by any other genus of flowering plants (Pennell, 1943, 1948; Li, 1948, 1951). Despite its high species richness and extremely diverse floral morphology, monophyly of *Pedicularis* is strongly supported in all analyses (Li, 1948; Tsoong, 1955–1956; Ree, 2005). Although some authors (Bonati, 1918, cited in Li, 1948) believed that hybridization is an important factor in the evolution of the genus, the number of proved hybrid species in the genus is low (Macior, 1982). Further investigation of the factors contributing to the great species diversity of this genus is needed. Our field investigation indicates that microenvironments might play a role in its evolution (Tang et al., observations), but the morphological diversity of corollas within the genus is believed to be related to diversity of pollination vectors (Pennell, 1943; Li, 1948; Macior, 1982). Specific pollination mechanisms might play a more important role (Macior, 1982). Therefore, the relationships between floral morphology of *Pedicularis* and pollinators have attracted the attention of researchers. However, mainly North American and European species have been studied (Sprague, 1962; Koeman-Kwak, 1973, 1979; Macior, 1982 and references

therein, 1983, 1986a, 1986b, 1986c, 1990, 1993, 1995a, 1995b, 1996; Williams and Batzli, 1982; Aluri and Robart, 1991; Eriksen et al., 1993; Philipp et al., 1996). In contrast to the considerable number of pollination ecology studies in North America, pollination ecology is known only for a number of species from northwestern Sichuan (Macior and Tang, 1997; Macior et al., 2001; Tang and Xie, 2006; Tang et al., 2007) and northwestern Yunnan (Wang, 1998; Wang and Li, 1998, 2005). This region (from the eastern Himalayas through northwestern Yunnan and western Sichuan to northwestern Sichuan) has been hypothesized as the center of origin (Hong, 1983) and the center of diversification of this genus (Tang et al., unpublished data). An investigation of the pollination ecology of more species from this region would enhance our understanding of floral and species diversity in *Pedicularis*.

Pedicularis is a high altitude genus in Northern Hemisphere mountain ranges. Most species of *Pedicularis* are distributed at 2500–4500 m in elevation, but previous pollination ecology studies of *Pedicularis* have only concerned species from 1600 to 3900 m in elevation, mostly within the 2500–3500 m range (Aluri and Robart, 1991; Macior, 1970, 1973, 1986b, 1990, 1995a, b, 1996; Macior and Tang, 1997; Macior et al., 2001; Tang and Xie, 2006; Wang and Li, 2005). With increasing altitude, growing season and blooming period of plants decrease, and the phenology of plant life cycles is delayed. Pollinator size, behavior, and caste are related to the phenology of plants in *Pedicularis* (Macior, 1983). However, little is known about the pollination ecology of *Pedicularis* species growing at elevations above 3500 m. This paper reports the results of a pollination ecology study of *Pedicularis muscoides* subsp. *himalayca*, a very low-growing subspecies, from Litang Xian (County), western Sichuan Province,

China. *Pedicularis muscoides* subsp. *himalayca* is one of a few extremely short species in the genus. Previous studies have indicated that some low species are adapted to pollination through elongation of the floral tube (Macior and Tang, 1997). In addition, richness of *Bombus* species decreases with altitude (Williams, 1998). The main objective of this study is, therefore, to study how the habit and floral morphology of this very low-growing alpine subspecies is adapted to insect pollination.

Materials and Methods

STUDY PLANT

Pedicularis muscoides H. L. Li consists of two easily distinguished subspecies: subsp. *muscoides* has a glabrous calyx, and subsp. *himalayca* Yamazaki has a calyx with dense glandular hairs. The former (typical) subspecies is endemic to western Sichuan, China, and study of herbarium specimens indicates that it grows only on Gongga Shan Mountain in western Sichuan. The latter subspecies has a wider geographical range. It was reported from Nepal and Mount Nyaso between Shigatse and Lhasa, Tibet, of western China (Yamazaki, 1986). This is the first record from Sichuan. This species is one of a few very short species of the genus (Tsoong, 1963). Its flowers were in full bloom when the observations began.

STUDY SITES

The pollination ecology of the plants was studied at two field sites in Litang Xian (County), western Sichuan Province, southwestern China, which is located on the southeastern part of the Qinghai-Tibetan Plateau. The main site (30.0000°N and 100.1893°E; elevation 4005 m) comprises an area of about 1 km², and is approximately 20 km from the county town. It is located on a northwest-facing slope near the 3137 km marker, along National Highway No. 318, which links Sichuan Province and the Tibet Autonomous Region (Xizang). The site was a large meadow consisting mainly of *Kobresia* spp. (Cyperaceae) and was grazed heavily by yaks and sheep (Fig. 1). The height of meadow plants averaged 5–10 cm. The slope gradient was 10–15° on the lower part and up to 20° on the upper part. *Pedicularis muscoides* subsp. *himalayca* was the dominant *Pedicularis* taxon. There were at least 12 patches of *P. muscoides* subsp. *himalayca*. A patch is defined here as a small population of plants which was separated from others by such factors as microenvironments, gullies, or scrub land. Other *Pedicularis* species that were in bloom included *P. lachnoglossa* Hooker f., *P. roylei* Maximowicz, and *P. ingens* Maximowicz, but they were scattered and far less abundant than the studied subspecies. Other associated plant species in bloom included *Polygonum milletii* (H. Léveillé) H. Léveillé (Polygonaceae), *Potentilla fruticosa* Linnaeus (Rosaceae), and *Rhododendron* sp. (Ericaceae).

The second site (30.0119°N and 100.2673°E; elevation 4193 m) comprises an area of about 200 m². It was on a mountain summit behind the county town of Litang. Due to this site's higher elevation and remote location far from roads, it was not grazed as heavily as the first site. The height of plants averaged about 40 cm. Species of *Pedicularis* growing at this site were *P. muscoides* subsp. *himalayca*, *P. anas* Maximowicz, *P. przewalskii* Maximowicz, and *P. floribunda* Franchet. Unlike the first site, *P. muscoides* subsp. *himalayca* was not the dominant *Pedicularis* species here, and it was common only in one patch. Other abundant plant species included *Allium przewalskianum* Regel (Liliaceae), *Gentiana macrophylla* Pallas (Gentianaceae), *Potentilla fruticosa*, *Ligularia lankongensis* (Franchet) Handel-Mazzetti (Compositae), *Stellera chamaejasme* Linnaeus (Thymelaeaceae), *Ranunculus* sp. (Ranun-

culaceae), *Aster* sp. (Compositae), and *Nardostachys chinensis* Batalin (Valerianaceae).

Twenty-three years of meteorological data from Litang, collected during the interval 1952–1980, indicate that temperature and rainfall are greatest during the month of July, with a mean annual temperature of 3.0 °C and annual precipitation of 726 mm. The mean monthly air temperature was 7.6, 9.6, 10.5, 9.8, and 8.1 °C for May through September, respectively, and monthly rainfall was 57.2, 150.2, 170.0, 158.0, and 107.5 mm for May through September, respectively. Furthermore, the first 10 days of July averaged the hottest temperatures (average = 11.1 °C) of the interval from late June to early August (SMB, undated).

OBSERVATIONS

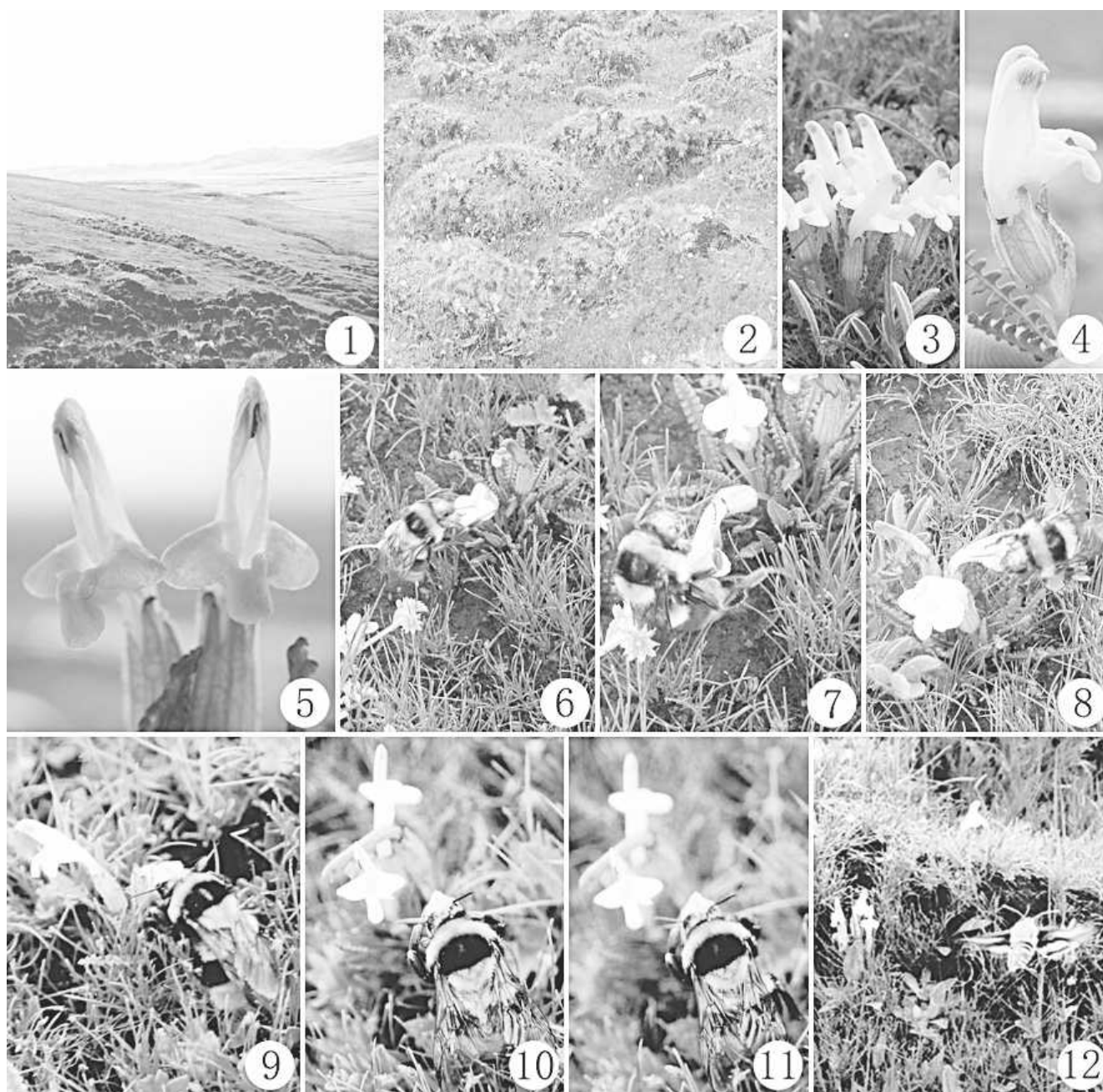
Field data were recorded by four investigators during 8–13 July 2003. All of the insects visiting flowers were collected whenever possible. Each observer was responsible for 1 or 2 patches of study plants. The distance between studied patches varied from 20 to 120 m. A total of six patches were observed: five at the main site and one at the second site. In total, 58 man-hours were spent observing the foraging behavior of insect visitors and collecting insect samples. Our previous observations revealed that few insects were active when the vegetation was wet and the temperature was low in the early morning. Observations during the study period started usually around 9:00–10:00 a.m. when the vegetation had dried of morning dew. Insect visits lasted until 4:30–6:00 p.m., when temperatures dropped considerably.

The methods applied in this study mainly followed those of Macior et al. (2001) and Tang and Xie (2006). Direct observations were made on *Pedicularis muscoides* subsp. *himalayca* and on insects visiting flowers at the study sites. Foraging behaviors of insects on *Pedicularis muscoides* subsp. *himalayca* were observed and recorded in the field on both photographic film and videotape. The numbers of bumblebee visits to flowers in the studied patches were recorded throughout the duration of the observations. Visits of an individual insect to different plants within a patch was considered as one visit. The frequency of visitation was based on the number of visits divided by the time period of observation, following Macior et al. (2001). Pollinators were collected from both the study plants and other associated plants in bloom at the two study sites.

To determine the percentage of full blooming flowers or withered flowers, three walks of approximately 100–200 m were taken at the main site when the study started (8 July 2003) and when most of the flowers had withered (13 July 2003). All of the 100 plants along the walks were counted, and their flowering condition was noted. The depths of 25 corolla tubes were measured on fresh materials in the field, from the base of the tube to a point where it divided into a dorsal galea and a lower trilobate lip. The plants were sampled randomly from four patches in the main site, and only flowers in full bloom were used to measure the corolla tube length. A portable refractometer was used to determine the total nectar sugar content deposited at the base of corolla tube of the full blooming flowers. The measurements were made in the morning before observation started. Each measurement of length was an average of five readings on a sample. For each refractometer measurement, nectar was taken by capillary from two or three flowers sampled randomly for the main site.

Temperature was measured on each study day when bumblebees were active, and at the time of day when bumblebee visits ended.

Collected bumblebee samples were pinned following conventional procedures for insect sample preparation, air-dried, and then



FIGURES 1–12. Habitat, flowers of *Pedicularis muscoides* subsp. *himalayca*, and foraging behavior of pollinators. Figs. 1–2. Habitat of *Pedicularis muscoides* subsp. *himalayca*, arrows indicating *muscoides* subsp. *himalayca*. Figs. 3–5. Flowers of *Pedicularis muscoides* subsp. *himalayca*. Fig. 3. Flowers. Fig. 4. Lower floral lip bent downwards. Fig. 5. Ventral view of galea showing ventral opening. Fig. 6. Queen bumblebee approaching flower with extended antennae to mouth of corolla tube. Fig. 7. Queen bumblebee grasping flowers. Figs. 8–11. Queen bumblebee standing on the ground and foraging on flowers with face and head entering corolla tube, with the stigma contacting with insect head in Figs. 9–10 and with yellow-haired thorax in Fig. 11. Fig. 12. A hawk moth hovering in front of *Pedicularis muscoides* subsp. *himalayca* with its glossa inserted into the corolla tube.

further dried for 10–24 hours using the heat from light bulbs when necessary. The weights and lengths of collected dried bumblebee samples were measured later in the laboratory. Each measurement of weight or length was an average of three readings on each sample.

Description of floral morphology was based on field observation of fresh materials at the main site. Bumblebee samples were identified to species and caste by Dr. Paul H. Williams of the Natural History Museum, London. Voucher specimens of bumblebees and plants were deposited at the Herbarium of Laboratory for Biodiversity and Environmental Studies, Department of Environmental Sciences, Sichuan University. Dupli-

cates of plant specimens were deposited at the herbarium of the Sichuan University, and duplicates of bumblebees were stored at the herbarium of the Institute of Zoology, the Chinese Academy of Sciences, and the Natural History Museum, London.

Results

ECOLOGY, FLORAL MORPHOLOGY, AND PHENOLOGY

Compared to the height of most other species of *Pedicularis*, *P. muscoides* subsp. *himalayca* was very small. Without its white flowers, this plant was difficult to see since the flowering plant was

TABLE 1

Corolla tube length and nectar sugar content in *Pedicularis muscoides* subsp. *himalayca*.

| Corolla tube length (mm) | | | | Nectar sugar content (%) | | | |
|--------------------------|-----------|------|-----|--------------------------|-----------|------|-----|
| N | Range | Mean | SD | N | Range | Mean | SD |
| 25 | 16.0–21.5 | 18.2 | 1.6 | 5 | 20.0–25.3 | 22.7 | 2.3 |

only 3–4 cm tall (Fig. 2). Stems were multi-branched at the base, clustered, and thin. All of the leaves were basal. Flowers were terminal and usually each stem had two flowers.

Pedicularis muscoides subsp. *himalayca* was often found in meadows that had been heavily grazed, mostly by yaks. Its occurrence seemed to be closely tied to microhabitats. Examination of its occurrence at six localities indicated that it grew mostly at well-drained but humid microhabitats. At very wet plots it grew on raised grassy tussocks (Fig. 2). At relatively less wet spots, it grew in depressions where moisture accumulated, implying that soil moisture and nutrients might be important factors in determining its distribution.

Other associated *Pedicularis* species in bloom, including *P. lachnoglossa*, *P. floribunda*, *P. roylei*, *P. ingens*, *P. anas*, and *P. przewalskii*, did not appear in the patches of *P. muscoides* subsp. *himalayca*. Their microhabitats were different and none of them was found in wet microhabitats. *Pedicularis lachnoglossa*, *P. ingens*, and *P. floribunda* were relatively tall and occurred in drier microhabitats. *P. roylei*, *P. anas*, and *P. przewalskii* were relatively low and appeared in relatively dry microhabitats. In addition, none of the above six species had the same corolla color as *P. muscoides* subsp. *himalayca*. The corolla of *Pedicularis ingens* was yellow but it was red to pinkish in the other five species. *Pedicularis ingens*, *P. floribunda*, *P. anas*, and *P. roylei* were nectariferous but *P. lachnoglossa* and *P. przewalskii* were nectarless.

Flowers were yellowish white, slightly or moderately out-curved from the apex of the calyx tube (at an angle of ca. 30–45°) (Fig. 3). Like the other species of the genus, the flowers were bilabiate. The upper lip (galea) was erect, toothless, and erostrate. There was a large, long opening along the ventral side of the galea (Fig. 5). The lower lip was trilobate and spreading (Figs. 3–5). The two lateral lobes were round and slightly bent downwards (Figs. 3–4), and the central lobe was smaller with a short stalk, slightly to strongly bent downwards (Figs. 3–4). The corolla tube was swollen at the apex where it divided into a dorsal galea and a lower trilobate lip, and where the flowers bent outwards, forming a more or less bag-shaped structure (Figs. 3–4). The style protruded from the tip of the galea. The protruding portion of the style was purple, and the stigma was purple or white. Anthers of the four stamens were concealed in the top portion of the galea. The top of the galea appeared dark colored because of the enclosed anthers (Figs. 3–4). No dark colored blotches were found on any parts of the flowers. Corolla tube depth varied from 16.0 to 21.5 mm; the average length was 18.2 ± 1.6 mm ($N = 25$) (Table 1). Copious nectar was deposited at the base of the corolla tube. The mean total sugar content was $22.7 \pm 2.3\%$, with a range of 20.0–25.3% ($N = 5$) (Table 1).

Ninety percent of flowers were in full bloom when our observations began on 8 July, suggesting that the flowering of most plants in the studied populations was closely synchronized. Some flowers withered during the course of our study (Figs. 6–8, 10–11), and by 13 July, approximately 90% of the flowers at the main site had withered. Only some of the plants growing in more moist conditions were still blooming. The blooming period of

TABLE 2

Species and caste of bumblebees collected from the study sites.

| Species | Caste | No. sample | Foraged plants/ground |
|--------------------------------|--------|------------|--------------------------------|
| <i>Bombus friseanus</i> | Queen | 13 | <i>P. muscoides himalayca</i> |
| <i>B. friseanus</i> | Worker | 1 | <i>Nardostachys chinensis</i> |
| <i>B. impetuosus</i> Smith | Queen | 1 | <i>Allium przewalskianum</i> |
| <i>B. kashmirensis</i> | Queen | 1 | <i>P. muscoides himalayca</i> |
| <i>B. ladakhensis</i> Richards | Queen | 2 | <i>Rhododendron</i> sp./ground |
| <i>B. lemniscatus</i> Skorikov | Worker | 1 | <i>Ranunculus</i> sp. |
| <i>B. lepidus</i> Skorikov | Queen | 1 | <i>Rhododendron</i> sp. |
| <i>B. patagiatus</i> Nylandder | Worker | 1 | <i>Allium przewalskianum</i> |
| <i>B. personatus</i> | Queen | 1 | <i>P. muscoides himalayca</i> |
| <i>B. rufofasciatus</i> Smith | Worker | 1 | <i>Nardostachys chinensis</i> |
| <i>B. skorikovi</i> (Popov) | Queen | 1 | Collected on the ground |
| <i>B. sushkini</i> | Queen | 1 | <i>P. muscoides himalayca</i> |

flowers appeared to be about 10 days. Peak flowering occurred in the first half of July, coinciding with the highest monthly temperature and rainfall of the year.

POLLINATORS, FORAGING BEHAVIOR, AND VISITATION FREQUENCY

Only bumblebees were observed to visit flowers of *Pedicularis muscoides* subsp. *himalayca*. A total of 11 bumblebee species were collected from the study sites (Table 2), including one species collected on the ground of the main site. Four bumblebee species [*Bombus friseanus* Smith, *B. kashmirensis* Friese, *B. personatus* Smith, and *B. sushkini* (Skorikov)] were responsible for pollination of *P. muscoides* subsp. *himalayca*. Among the collected bumblebee samples, *Bombus friseanus* was the most common and frequent pollinator of the study plants, and 13 of the 16 bumblebee samples (81%) collected on *P. muscoides* subsp. *himalayca* were *B. friseanus*. Only one sample each was collected for the other three species. Other bumblebee species were collected from *Nardostachys chinensis*, *Allium przewalskianum* Regel, *Rhododendron* sp., etc. or on the ground (Table 2) of the main site, respectively.

Twenty-one of the 25 collected bumblebee specimens were queens, and the remaining four were workers (Table 2). Only queen bumblebees were observed visiting the flowers of *Pedicularis muscoides* subsp. *himalayca*. Worker bumblebees did not visit *P. muscoides* subsp. *himalayca* at all, but visited other associated plant species (Table 2). The average body weight of the dried queen bumblebees collected on *P. muscoides* subsp. *himalayca* was 244.4 ± 34 mg (range of 160.0–281.3 mg). The average length of the specimens was 28.7 ± 3.2 mm (range of 20.3–33.0 mm) (Table 3). The average body weight and length of the four worker bumblebee samples were 31.7 ± 12.7 mg and 13.9 ± 2.0 mm, respectively (data not presented).

Only one of the 16 queen bumblebees collected on *Pedicularis muscoides* subsp. *himalayca* carried pollen loads, implying that the queen bumblebees foraged on *P. muscoides* subsp. *himalayca* for nectar. Based on direct observations, corroborated and extended by photographs and videotape

TABLE 3

Body weight (mg) and length (mm) of collected bumblebee queens.

| | Range | Mean | SD |
|-------------|-------------|-------|------|
| Body weight | 160.0–280.0 | 244.4 | 34.7 |
| Body length | 20.3–33.0 | 28.7 | 3.2 |

records, the queen bumblebees pollinated the flowers nototribically. The queen bumblebees approached flowers with antennae extended toward the mouth of the corolla tube (Fig. 6), or grasped the flower (Fig. 7), and would enter their proboscides into the corolla tube (Fig. 8) while trying with their hind legs to support themselves on the ground or sometimes on the plants. Assuming this position, the bee then entered its head into the corolla mouth, forcing it into the corolla tube to imbibe nectar located at the base of the corolla tube (Figs. 8–11), bending the flowers downwards (Figs. 7–8). During this behavior, the insect's head rubbed the galea top containing the anthers and white pollen clouds were seen to be deposited on the insect's face and head. After visiting 3–5 flowers, the queens stood with hind legs on the ground and groomed pollen from their tongues and head into pollen baskets. When the insect extended itself further into the corolla tube, the stigma was usually directed to, and rhythmically contacted, the densely hairy portion on the back of the thorax (Figs. 9–11). Because the stigma extruded out of the galea, it first contacted the residual pollen on the head and thorax of the insect. Then the pollen of the same flower showered onto the insect's head and thorax when it entered into the corolla tube, which squeezed the galea containing the anthers to release or to scrape pollen. When this same queen bumblebee positioned itself on the next flower, her pollen-covered head and thorax touched the protruding stigma, thus performing pollination.

Frequency of bumblebee visitation to the study patches varied considerably, from 0 to 4.3 bees h^{-1} . Bumblebee activity was closely related to air temperature. When the temperature was low (e.g., below 12°C), no bumblebees visited flowers within a period of 4 hours or even for a whole day. The weather fluctuated considerably during the study period. The temperature increased from 10 to 16 °C or dropped from 16 to 12 °C within a period of 1–2 hours. When the temperature dropped to approximately 12 °C, mobile bumblebees paused in their foraging or flying activities and remained on the ground. Some queens that we collected were found on the ground in a state of torpor. Bumblebees resumed their activities when the temperature rose to 15–16°C. Bumblebees visited flowers frequently when the temperature was favorable for flying activities (i.e., over 16 °C).

Only once was a hawk moth (*Celerio* sp.) observed hovering in front of *Pedicularis muscoides* subsp. *himalayca* flowers (Fig. 12) for nearly two minutes, inserting its glossa into the corolla tube to imbibe nectar. Its flight speed was considerable. When disturbed, it flew away very quickly. The hawk moth foraged on and possibly nototribically pollinated flowers of *P. muscoides* subsp. *himalayca*.

No bumblebees or other insects were observed to visit the other six *Pedicularis* species during the study period. However, both queen and worker bumblebees visited *Allium przewalskianum*, *Nardostachys chinensis*, *Ranunculus* sp., and *Rhododendron* sp. in an upright position (Table 2). These species were nectariferous; that is, bumblebees foraged on them for nectar.

Discussion

Pedicularis muscoides subsp. *himalayca* flowers were exclusively pollinated by queen bumblebees. They consistently foraged on the flowers for nectar and appear to have effectively pollinated the flowers. All of the previous pollination ecology studies in *Pedicularis* have revealed bumblebees as the principal pollinators. All the nectariferous species thus far studied were pollinated by both queens and workers of bumblebees and no species have been reported to be pollinated only by queen bumblebees (Aluri and

Robart, 1991; Macior, 1970, 1973, 1975, 1978, 1983, 1986a, 1986b, 1988, 1995a, 1995b, 1996; Wang and Li, 2005). The exclusive pollination of *P. muscoides* subsp. *himalayca* by queen bumblebees appears to be the result of coadaptation of *Pedicularis* species and bumblebee pollinators. The plant habit, floral presentation, floral morphology, and phenology of *P. muscoides* subsp. *himalayca* appear to be well adapted to pollination by queen bumblebees.

As a result of the apparent coadaptation between *Pedicularis* and *Bombus*, flowering phenology of *Pedicularis* is related to bumblebee colony development and queen bumblebee-pollinated species are always nectar producing (Macior, 1982). Blooming period is associated with the types of inflorescences and number of flowers. The closely synchronized or nearly simultaneous blossoming of *P. muscoides* subsp. *himalayca* flowers is essential, given the short flowering and growing period and highly fluctuating weather in the study region. Unlike most species of *Pedicularis* that have many-flowered racemose or spicate inflorescences, *P. muscoides* subsp. *himalayca* usually has two terminal flowers. For plants with few flowers, a high degree of synchronicity in flowering may be considered an adaptation to maximize insect pollination and hence reproductive success (Mendez and Diaz, 2001). Foraging activities of bumblebees in the study region are reduced by usually low and fluctuating air temperatures. Bumblebees forage on *Pedicularis* only when the temperature is relatively high. Low temperature decreased pollinator activity, which has also been observed in other areas (Aluri and Robart, 1991; Bergman et al., 1996). The blossoming feature of *P. muscoides* subsp. *himalayca* is probably an adaptation to the limited growing season and limited period of pollinators' activity at high elevations since queen bumblebees usually forage on flowers only for a short period of time (Macior, 1982). Highly synchronized or almost simultaneous blossoming in *P. muscoides* subsp. *himalayca* helps attract bumblebees. Bumblebee visits to other nectariferous but much scattered *Pedicularis* species in the study sites were extremely rare.

Angiosperms have developed a broad range of reproductive strategies, and the morphology and phenology of the flowers will influence the behavior of the pollinators. The occurrence of pollination patterns is apparently associated with the phenology of pollinator foraging behavior and forager size. Foraging behavior of pollinators is often determined by the floral characteristics of plants (Howe and Westley, 1997). Floral morphology, plant height, and orientation of flowers in *Pedicularis* might enhance pollination efficiency. For instance, the elongation of the very long corolla tube in the low plant *P. longiflora* Rudolph var. *tubiformis* (Klotzsch) P. C. Tsoong was thought to attract pollinators (Macior and Tang, 1997). The very short plant height of *P. muscoides* subsp. *himalayca* might also be an adaptation to pollinators and their foraging behavior. The laterally expanded, trilobate lower lip of the corolla usually provides support for the pollinator while it is foraging in an upright position (Macior, 1973). This is not exactly the same as the observation in the present study. This subspecies is pollinated exclusively by queen bumblebees. If it grew taller, it would be difficult for the thin plants to support the queen's weight and to counteract the force the queen exerts on the plant while trying to enter the corolla tube. As observed in the field, all the flowers bent to the ground during the queen bumblebee's foraging activities, and the queen bumblebee supported its body with its hind legs on the ground or on the plants, but not on the lower corolla lip as observed in many other species (Macior, 1982). The corolla morphology and floral presentation seem also to be well adapted to queen bumblebee pollination. The more or less bag-shaped, swollen corolla tube appears to be adapted to queen bumblebee pollination. If small-sized worker bumblebees visited the flower,

it would be easy for the insects to enter the corolla tube but they would only occasionally pollinate the flowers because the stigma would only infrequently contact the insects. The outcurved, bilabiate corolla and bent central lobe of the lower lip enable easy access to the flower by queen bumblebees. The body length of queens (ca. 3.0 cm) is comparable to the height of *P. muscoides* subsp. *himalayca* (3–4 cm with flowers). The body length of a queen bumblebee enables it to easily reach the corolla mouth and enter the corolla tube to imbibe nectar at the base of the corolla tube when the bumblebee uses its hind legs for support on the ground or on the plants. The outcurved flowers can further facilitate the visitation of bumblebee queens. It would be interesting to study the relationship between the presentation of flowers and the pollination efficiency in other species, largely neglected in previous studies.

Collection of pollen and nectar from the same species by the same insect was done through separate actions in many plants. A number of studies of *Pedicularis* have reported that the same insect may first collect nectar by one action and then pollen by another action, or vice versa (Meidell, 1944; Macior, 1966; Olesen, 1996; Koeman-Kwak, 1973; Maloof and Inouye, 2000). In the present study, however, nectar and pollen were collected through only one action. The flowers of *P. muscoides* subsp. *himalayca* offer both nectar and pollen during a single insect visit. This should help enhance pollination efficiency.

Pedicularis is characterized by having both many species and highly diverse corolla morphology (Pennell, 1948; Li, 1948, 1951; Tang and Xie, 2006). Although there is considerable diversity within the genus, little pollination variability has been reported to date, which fails to support the hypothesis (Pennell, 1948; Li, 1948) that pollinators of this genus would be as diverse as the plants' corolla morphology. Pollination ecology studies of *Pedicularis* in North America (Macior, 1982 for review of earlier studies, 1983, 1986a, 1986b, 1986c, 1990, 1993, 1995a, 1995b, 1996), Europe (Koeman-Kwak, 1973, 1979; Eriksen et al., 1993), Japan (Macior, 1988), the Indian Himalayas (Macior, 1990; Macior and Sood, 1991), and the Tibetan Plateau (Macior and Tang, 1997; Wang, 1998; Wang and Li, 1998, 2005; Macior et al., 2001; Tang and Xie, 2006) have revealed only bumblebees as the principal effective pollinators of *Pedicularis*, although hummingbirds (Macior, 1986c), hawk moths, and honeybees (Macior and Tang, 1997; Macior et al., 2001) also forage on some species of *Pedicularis* that are principally pollinated by bumblebees. In addition, lepidopteran insects with long proboscises were thought to pollinate very long-tubed species (Li, 1948). However, they were found to pollinate only the nectariferous species with short corolla tubes (this study; personal observation of other species). All of the long-tubed species are nectarless and are pollinated exclusively by bumblebees (Macior and Tang, 1997; Wang and Li, 1998; Macior et al., 2001; unpublished observations). Pollination of *Pedicularis* by hawk moths was reported only once in North America (Macior, 1982). The foraging behavior of hawk moths in western Sichuan, China, is similar to that of hummingbirds in North America (Macior, 1986c), but the mechanism is different. Hummingbirds foraged nectar that is not available to bumblebees (Macior, 1986c), but based on our study, hawk moths apparently compete with bumblebees for nectar. Due to a short flowering period, no detailed foraging behavior of hawk moths was observed. Based on the observation of hawk moths' behavior on other nectariferous species (personal observation), the hawk moth is probably an ineffective and occasional pollinator since its proboscises are fine and slender. The contact of the proboscises with stigma would be only occasional. If hawk moth visits decrease the available nectar, queen bumblebee pollinators would

have to increase their foraging area to gather the nectar they need (Maloof and Inouye, 2000), which would increase the total number of plants visited. However, further study of the relationship between hawk moths and *Pedicularis* is needed.

The most variable element of corolla morphology in *Pedicularis* is found in the galea (Li, 1948; Tang and Xie, 2006). Li (1951) suggested that evolution of the galea is from an unbeaked form to one with a long and strongly contorted beak (rostrum). In general, the unbeaked species are nectariferous and are mostly pollinated nototribically by nectar collecting foragers. They are less commonly pollinated sternotribically by pollen collecting bumblebees, while the species with galea of long and strongly contorted rostrum are nectarless and exclusively pollinated sternotribically by pollen collecting foragers. Enhancement in pollination efficiency might be the driving force of corolla morphology evolution. Studies so far have revealed four groups of pollinators: bumblebees, honeybees, hummingbirds, and hawk moths. They all pollinate unbeaked and nectariferous species, but only bumblebees are known to pollinate the nectarless species with a long and contorted rostrum (Macior, 1982; Macior and Tang, 1997; Macior et al., 2001; personal observations), which suggests that the more advanced species may be pollinated by a sole group of insects. Although there is no fidelity relationship between *Pedicularis* species and their pollinator species, the developmental tendency to fidelity is obvious. The primitive species in *Pedicularis* are all unbeaked (Li, 1951) and nectar producing. They are pollinated by worker bumblebees, queen and worker honeybees, hummingbirds, and hawk moths. The advanced species in *Pedicularis* are beaked and nectarless. The most advanced species have a long corolla tube, long and strongly contorted beak, and are nectarless. The nectarless species are mostly pollinated only by worker bumblebees. Further study on the relationships between different types of pollinators and the evolution of floral morphology is needed.

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